HIBERNATION OF THE THIRTEEN-LINED GROUND SQUIRREL, *CITELLUS TRIDECEMLINEATUS* (MITCHILL). III. THE RISE IN RESPIRATION, HEART BEAT AND TEMPERATURE IN WAKING FROM HIBERNATION.[1]

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Introduction.

The present study was taken up from 1915 to 1918 before the reports on waking of European rodents and bats (Horvath, '72, '78; Pembrey, '01, '03; Dubois, '96; Polimanti, '12; and others) had come to the attention of the author. While on this account many of the facts have been discovered independently by the author, the whole study has been reworked since investigation of the waking process was resumed in 1924, and it is here presented not only for its own value, but also in comparison with the work of others and as fundamental in the further study of hibernation and its possible causes. Brief reports on waking in a few individual ground squirrels have been given by Hahn ('14), Shaw ('25) and others, but the variability which has been found in the waking process has made an extended study necessary before any general description of it under different conditions of temperature and stimulation could be made.

In the first paper of this series (Johnson, '28) the conditions in hibernation and in normal activity were compared. The second paper (Johnson, '29) described two types of waking: (*a*) a relatively rapid awakening accompanied by trembling, following a *disturbing* of the animal by removing it from the nest and laying it on its side or back; (*b*) a more gradual awakening, usually without trembling, following removal *without disturbance* to a warm room, or following some handling after which it was placed back in the nest in the rolled-up position, and not removed from

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the cold room. In this type of awakening the raising of the head, the opening of the eyes and the moving forward often occurred about the same time, the state of hibernation apparently passing over gradually into normal sleep from which the animal awoke from some stimulus, external or internal. This is probably the type of waking found in nature, whereas the disturbed kind is that usually described in the literature.

This paper deals with the changes in respiration, heart beat and temperature in what must be considered the disturbed type of wakening, because the taking of the heart beat involved either the unrolling, or a more vigorous handling, of the animal.

Animals and Methods.

Some *Citellus tridecemlineatus tridecemlineatus* (Mitchill) and many *C. t. pallidus* (Allen) animals were used. The lower rate of heart beat which could not be obtained with a stetoscope, was secured by the use of a needle. At a rate of about 100 beats a minute the needle was removed and the stethoscope used. Some records were also taken by means of an electrocardiograph. It was hoped to obtain records of rise of heart beat in *undisturbed,* rolled-up animals with the electrocardiograph, but the placing of electrodes on the forelegs above the elbows apparently disturbed them even more than the needle, which could be inserted readily through the thoracic wall into the heart muscle after gently unrolling the animal and laying it on its back. For this reason the needle method appeared preferable and most of the heart beat records were taken with it. Temperatures were taken with small especially constructed thermometers but usually thermoelectrically, chiefly in the food pouch because this involved almost no stimulation. (See Johnson, '29, for further details of methods, and see discussion of Fig. 3, this paper, for further reasons for using pouch temperatures. As methods were modified in the progress of the work some discussion of them will be given within the paper.)

Miss Virginia Hanawalt, Messrs. Earl Herrick, E. Duane Sayles, Robert T. Hill and Mrs. Joanna Challans have assisted in various phases of the work. Dr. Ralph Major, of the University of Kansas Medical School, kindly extended the use of an

electrocardiograph and he and his assistants aided in taking some heart beat records with this apparatus.

Changes in Respiration Rate in Waking from Hibernation.

From a rate of one half to four a minute in deep hibernation (Cf. Johnson, '29) the respiration increased distinctly in rate when the animal was disturbed and, as is seen in the graphs in Fig. 1, this increase usually continued till near the time of opening of the eyes, when very commonly the rate was about 150 a minute and usually ranged between 100 and 200 a minute. At about the time of opening of the eyes the respiration rate often fell distinctly if the animal was quiet. The very rapid shallow inspirations common in normal excited animals were not observed in awakening from hibernation. The graphs (Fig. 1, I.) show much variation in the rate of increase from minute to minute. This irregularity suggests the presence of a coarsely adjusted respiratory regulating mechanism, stimulation of which may produce over-aëration of the blood followed by decreased respiration for several seconds or even minutes. Such periods of decreased respiration following rapid respiration sometimes lasted as long as 30 or 40 minutes in animals awaking undisturbed in a warm room. No graphs are shown of these animals because heart beat and temperature records were not taken of them.

A definite correlation between rate of increase of respiration and higher room temperature is seen in the three groups of graphs in Fig. 1. The curves in I., *a*, taken in a room of about 2 to 12° C. rise slowly; those in I., *b*, taken in a room of 15 to 22° C., rise more rapidly; and those in I., *c*, from a room of 25 to 35° C., rise most rapidly.

Simultaneously with respiration there was taken the heart beat (Fig. 1, II., *a, b, c*) and temperature (Fig. 1, III., *a, b, c*). These animals were therefore disturbed slightly by a thermocouple in the food pouch and more by being laid on the back so that the needle might be inserted into the heart. They were also exposed more to the surrounding warm air in *b* and *c* (curves *E–L*) than if they could have been left rolled up. To avoid these sources of stimulation some records of respiration and temperature alone were taken, with the animal replaced in the nest rolled up in its natural position after the thermocouple was gently inserted into the food pouch. The head therefore was underneath and next to the cold wood shavings which constituted the nest. One of these

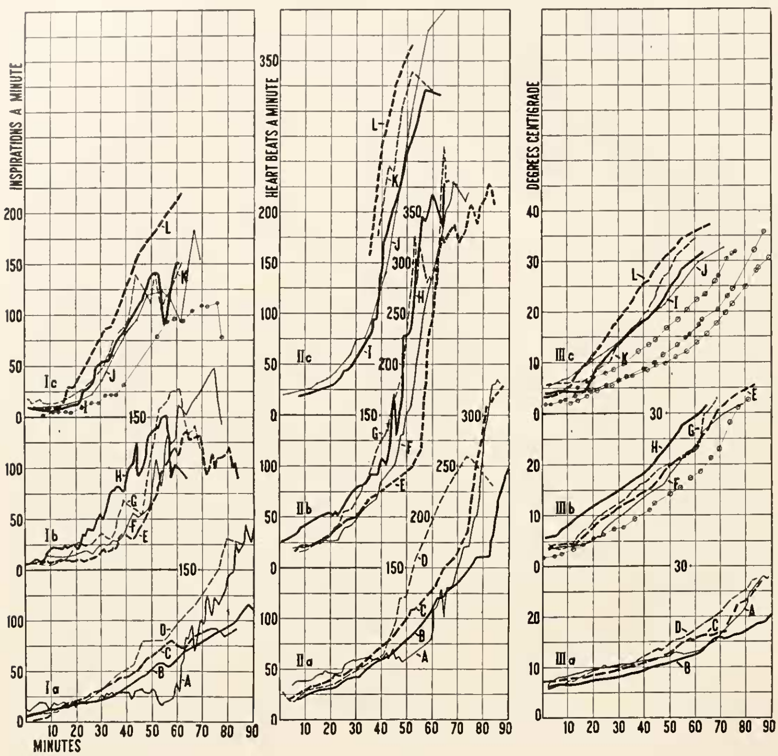

FIG. 1. Graphs of increase in respiration (I.), in heart beat (II.) and in temperature (III.), in a cold room of about 2° to 10° C. (*a*), in a room of about 15° to 22° C. (*b*), in a warm room of about 25° to 35° C (*c*). The curves belonging to one animal are designated by the same capital letter, thus I., *a A*, II., *a A* and III., *a A* represent the respiration, heart beat and temperature increases respectively in one waking in the cold room of the animal *A*. The fine lines connecting the rings in I., *c*, II., *b* and II., *c* are graphs of animals waking relatively undisturbed (thermocouple gently placed in the food pouch and the animal replaced rolled up in the nest). In the other graphs the animals were disturbed by being straightened out and by taking of heart beat in addition to temperature.

curves of relatively undisturbed awakening in a room of 23° C. was between *E* and *G* (Fig. 1, I., *b*). One in a room of 29° C. almost paralleled, but rose later than, *I* (Fig. 1, I., *c*). Another showed almost no rise for 50 minutes, then rose parallel to *I* in Fig. 1, I., *c*. A fourth, which rose about half way between the two mentioned, is shown with dots within circles in Fig. 1, I., *c*. The rolled-up position and the probable shortage of air together with the lack of continued stimulation, because of its normal position, probably accounted for the slow rise of the curve at first. Respiration curves of animals not disturbed but merely brought to a room of warm temperature lagged from about five to twelve minutes behind those shown, but paralleled them when the rise once started. In some such animals there were long periods of very slight respiration lasting from 10 to 20 or more minutes.

Changes in Heart Beat in Waking.

The heart beat of animals left in the cold room after inserting a needle through the thoracic wall into the heart sometimes failed to rise or even fell rarely in rate for a short time, but usually there was a gradual increase at first followed by a much greater increase in the latter part of the waking process as in Fig. 1, II., *a*. A few animals had a rapid rise within 20 minutes of the time they were disturbed. Such an early rise usually indicated that the animal was not very torpid.

When animals were transferred to a warm room of about 20° C. (Fig. 1, II., *b*) the rapid rise in heart beat and the peak of its rise both came sooner than in the cold room. The rise was still more rapid and the peak reached still earlier in animals taken to a room of about 29° C. (Fig. 1, II., *c*). Under all conditions of waking the heart beat was very rapid about or a little after the time of opening of the eyes and some records of 400 beats a minute were taken with a stethoscope. The rate fell shortly after this. The very rapid increase in rate just before opening of the eyes was not produced by holding the animal because it appeared in those animals which were not held before the eyes were opened. It did not appear to be produced by the pressure of the stethoscope against the thorax, because the same rise occurred in the records taken with the electrocardiograph (Fig. 5) where there was no stimulation of the animal except the pressure of the electrodes on the forelegs. Other evidence presented later in this paper also indicates that stimulation is effective only to a limited extent in speeding up the waking process and it appears very probably that there is always quite a marked rise in heart beat at this time in the disturbed type of awaking even if there is no stimulation at and just before the opening of the eyes.

In Fig. 1, II., *c*, *K* and *L*, two records taken with the stethoscope only are given, showing that the heart beat taken with a needle is similar in the latter part of the waking process at least to that in animals on which no needle was used.

The Rise of Temperature in Waking from Hibernation.

a. Comparisons of Œsophageal, Food Pouch, Deep Rectal and Anal Temperatures.—Graphs made of temperatures taken simultaneously in different regions of the body during waking from hibernation confirmed the observations of Dubois ('96) and others that the region near the heart warms up most rapidly. This is evident in Fig. 2, where it is seen that the deep œsophageal temperature (thermocouple inserted 5 cm. in from front of mouth, which would be to a point near the heart) rose slightly more rapidly than the temperature taken in the lower food pouch, as the animal lay on its side, which follows it very closely. The deep rectal temperature taken at a depth of 4 cm. and the anal temperature taken at a depth of 1.0 to 1.5 cm. showed almost no increase for some minutes and both lagged far behind the œsophageal and pouch temperatures until these two had almost reached their maximum some time after the animal opened its eyes and was able to move about. The anal temperature rose more slowly than the deep rectal. At other depths both in the œsophagus and in the rectum or colon slightly different curves than those shown would result. What is strikingly shown by this and five other graphs that agree with it is that the source of heat is in the thorax and as the heart and respiratory muscles are the ones which are contracting, it is evident that they are producing the heat. It is also clear that there is a marked distribution of this heat in the anterior part of the body since the pouch temperature follows that of the deep œsophagus closely but that there is a very slow diffusion of the heat to the abdomen, especially to the posterior abdomen, probably through a lack of circulation there. It is therefore a question where the temperature should be taken during the waking process.

Five other sets of graphs agree with those shown in Fig. 2 in that the pouch temperature is close to that of the œsophagus (maximum differences of 2°, 2°, 3°, 3° and 3°, respectively) in all cases

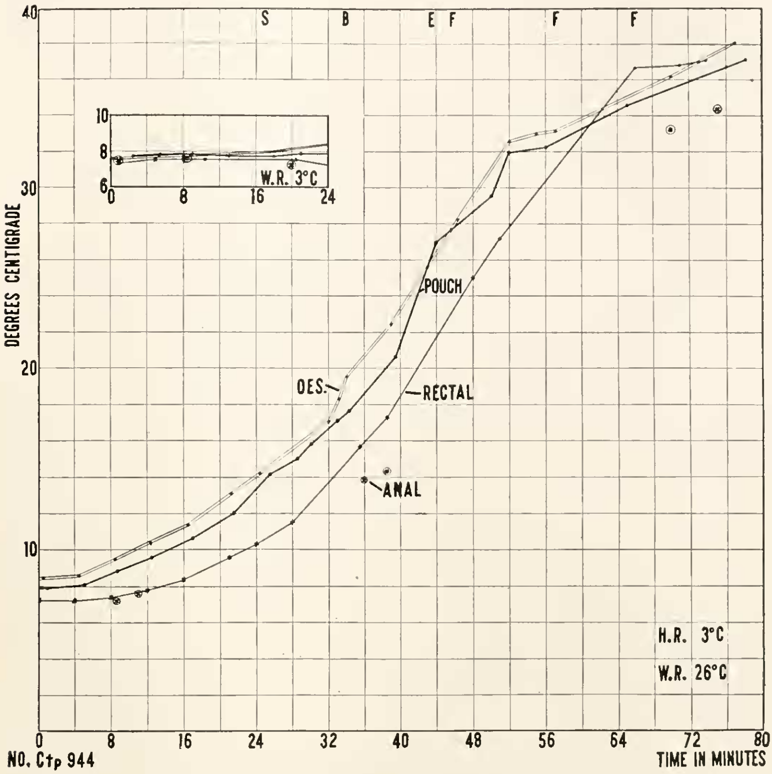

FIG. 2. Curves of the rise in temperature in the œsophagus (*œs.*) at a point 60 mm. in from the tip of the nose, in the food pouch (pouch), 43 mm. in the rectum (rectal), and 10–12 mm. in the anus (anal), all in one waking of *C. t. pallidus* 944. The insert gives observations in the cold room in which the animal was hibernating; and the main graph, the observations in the warm room. *H. R.*, hibernating room; *W. R.*, waking room; *S*, struggling; *B*, deep rapid breathing; *E*, eyes opened; *F*, fighting so that it had to be held or held down against the nest for the observation at that time. Note that the temperature of the pouch follows that of the œsophagus more closely than do the other two.

following the œsophageal temperature more closely than did deep rectal or anal temperatures. In Fig. 3 the anal temperature is almost the same as the deep rectal in the cold room (see insert,

Fig. 2) and also for a time after removal to a warm room (main graph, Fig. 2). Only one of the other five graphs agrees with this. Four of them show that the anal temperature rose somewhat more rapidly at first (probably affected by the warmth of the room) and rather late in the waking period the deep rectal temperature rose above the anal. On account of this fluctuation and even more on account of the lag in the curves which prevents them from registering a change in heat production in waking, temperatures taken in the anus or rectum are not nearly so indicative of internal temperature as are either those of the pouch or the œsophagus.

In Fig. 2 the rise of the pouch and rectal above the œsophageal temperature was an irregularity not found in the other graphs and was probably produced by some unusual conditions, as the struggling of the animal at these times, or the use of a different thermocouple, one which was protected against biting, in the last part of this record.

It is evident that the deep œsophageal region near the heart is the center of heat formation and temperatures taken there would be very valuable if the animal were not disturbed in taking them. However, when records of relatively undisturbed awakening are desired œsophageal temperatures are out of the question. Pouch temperatures, while affected somewhat more by external temperatures than œsophageal temperatures, following œsophageal temperatures quite closely and doubtless are even more indicative of the internal temperature of the animal than is shown in the graphs which include also the œsophageal temperature, because pouch temperatures when taken alone can be secured with practically no handling and also because the thermocouple in the œsophagus stimulates the heart and respiratory muscles thereby causing the œsophageal temperature to rise abnormally fast, especially early in the waking period when waking is otherwise usually slow. It seems therefore that pouch temperatures taken with care give the rise of temperature in waking (produced by warming the animal or by disturbing it slightly at first) more accurately than does any other.

b. Rise of Temperature in Waking in a Cold Room of About 2° to 10° C.—Slight handling and the insertion of a thermometer bulb in the cheek pouch would produce waking in the cold room, and even very gently inserting a fine thermocouple into the cheek pouch would often but not always produce waking. In these studies the animal was held only when necessary and only late in waking. The process of waking in a cold room was studied in 12 graphs, four of which are given in Fig. 1, III., *a*. These four are selected to show the various types of curves rather than the most prevailing type. There was usually a slow rise in temperature for some time, then a rapid rise towards normal temperature, which was then approached more gradually, giving an S-curve somewhat similar to those illustrated by Dubois ('96) for the marmot. The temperature finally became fairly stationary if the animal was undisturbed, or continued to rise for some time if handled considerably (see Johnson, '28, for effect of handling). Variation in some of the waking curves was observed. In one the temperature rose almost uniformly during the whole period. In another there were two periods of rapid rise. In some graphs and in some records of not awakening where the animal was removed to a colder room the pouch temperature fell at first, and the internal temperature probably also did in these cases for the animals became more inert. When œsophageal temperatures were taken they rose steadily from the first because of the stimulation produced by the thermocouple, even when the pouch temperature was found to drop at first.

c. Rise of Temperature in Waking in a Room of 15° to 22° C.—Sixteen graphs were made of waking in a room of intermediate temperature, four of which are shown in Fig. 1, III., *b*. The effect of the warm surrounding temperature was evidenced by an increase in the rate of rise of the animal's temperature within a few minutes after the animal was removed from hibernating quarters to the warmer room. The rate of rise was not always rapid at first (Fig. 1, III., *F*), but in some cases it was slightly more rapid than near the time the animal had reached the temperature of the room (*H* and *E*), and quite frequently the curve approached a straight line.

To determine to what extent the rapid rise of temperature of the animal in a warm room was caused by the higher external temperature two dead animals were removed from the cold room to a warm room of about 25° C. One showed a marked rise in pouch temperature very similar to curves *E, G* and *H* (Fig. 1, III.) for the first 25 minutes. In the other the anal and pouch temperatures rose very close together and more rapidly at first than the deep œsophageal and deep rectal (4 cm.), but all rose more slowly than *E* and *G*. In all cases as the room temperature was approached the rise became slower.

From these and one more record in a warmer room, it is clear that the rapid rise in temperature of a torpid animal for the first few minutes after it is brought into a warm room is produced chiefly by the higher external temperature. As time passes the metabolism is greatly increased and becomes the chief cause and finally the only cause of further warming of the animal.

From the latest records taken it appears that curve *F* is characteristic of temperatures taken in a food pouch under the animal whereas curves *E, G* and *H* are more typical of those taken in the food pouch which was away from the nest. The four curves (*E–H*) were taken with the animals lying on the back with the food pouch away from the nest except probably *F*. Curve *F* is also quite similar to deep œsophageal temperatures as seen in seven graphs. An eighth graph of œsophageal temperatures formed a straight line.

d. Rise of Temperature in a Room of About 25° to 35° C.—Eighteen pouch temperature graphs of animals transferred from the refrigeration room to a warm room were made and studied. Some of the different types found are illustrated in Fig. 1, III., *I, J, K,* and *L*. A few of the curves (see *I*) had a period of rapid rise at first and one near the time of opening the eyes. Later work indicated that this is produced when the pouch is rather open causing warm air to enter the pouch. When a thin thermocouple was used and precautions taken not to force the mouth open most of the curves formed almost a straight line (*L*) or sometimes they rose slowly for a few minutes and then gradually more rapidly (*J, K*), especially shortly before opening the eyes, until the animal was awake, when the rate of rise slowed down and finally ceased.

e. Rise of Temperature in Relatively Undisturbed Awakening.—After gently inserting a thin flexible thermocouple into the food pouch of a torpid animal it was replaced in its nest in the rolled up position. This was done just before or just after removing the animal to a warm room. Heart beat was not taken in these animals. The temperature records are given in Fig. 1, III, *b* and *c* (dots connected by fine lines). With the head underneath against the cold nest and also with lack of stimulation from unusual position the rate of rise of temperature is quite slow at first resembling somewhat the curves of temperature of waking in a cold room.

Correlation of Respiration, Heart Beat and Temperature Rise in Waking from Hibernation.

In order to study the relations between the rise in respiration, heart beat and temperature, graphs of all three were combined from a single waking process initiated by slight handling or transference to a warm room. These combination graphs show correlations between the three curves, which rise more or less together. Waking in a cold room (0° to 8° C.) showed a very gradual rise in heart beat and respiration following insertion of a thermocouple for taking temperature and of a needle for counting heart beat (Fig. 3). The rise in temperature was even slower. In Ctp 128 the temperature fell for about the first seven minutes during which temperature was taken, for the animal had been transferred from a surrounding temperature of 6° C. to a waking room temperature of 0.2° C. (rising to 4° C. near the end of the awakening period) but the increasing heart beat and respiration maintained the temperature of the animal for the next ten minutes after which there was a slow but gradual rise similar to that in Ctp 740. In both of the graphs in Fig. 3 there are some irregularities in the temperature rise. In the curve for Ctp 740 the rapid rise at 68 and 71 minutes was evidently produced by vigorous fighting by the animal against the insertion of the thermocouple into its pouch. Ctp 128 was biting and fighting fiercely with the observer's hand just before it opened its eyes at 108 minutes, resulting in an unusual rise in pouch temperature followed by a drop such as was seen in no other graph. It is evident that when an animal is vigorously using its jaw muscles that an unusually high temperature might prevail in the cheek pouch for a few minutes, but the distribution of this heat over the body would soon cause a drop in the pouch temperature to near the average temperature of the anterior portion of the body. In the case of Ctp 740 the animal returned into hibernation and a second waking record was obtained under almost the same conditions of temperature. The graph was almost identical to that shown in figure 3.

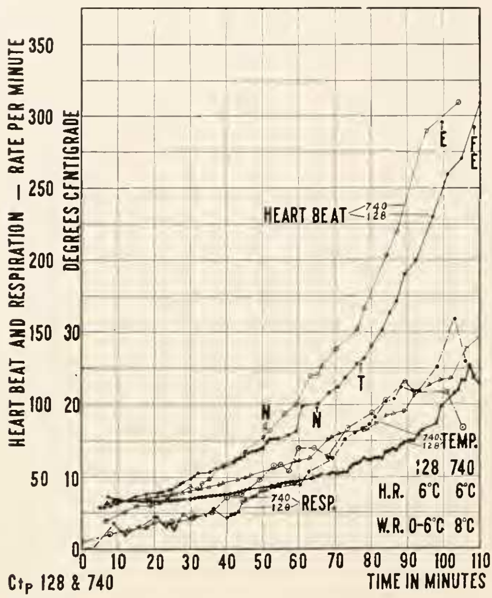

FIG. 3. Curves of rise in respiration, heart beat and temperature combined for study of correlations between them. Both *C. t. pallidus* 128 and 740 were removed from a refrigerator (H. R.) of 6° C. at 0 minutes and observations were immediately begun in rooms of 0° (rising to 6° by end of the record) and 8° C. respectively. *N*, needle removed and stethoscope used; *T*, trying to turn over; *E*, eyes opened; *F*, fighting. The dots on each graph indicate the actual readings taken.

Figure 4 gives the records of two animals waking simultaneously in a room of 30° C. under the same conditions except that no needle was used on animal Ctp 932. A general correspondence in rate of rise is seen for the three processes in each animal and also between those of the two animals. Ctp 932 was distributed five minutes later than Ctp 947 but it had a higher initial temperature so that its waking process was slightly the more rapid of the two. If the curves of Ctp 932 were moved to the right until the initial temperatures of the two animals correspond then the temperature and heart beat of the two would be almost identical. The respiration curve of Ctp 932 would lag behind at first but be higher at the end than that of Ctp 947.

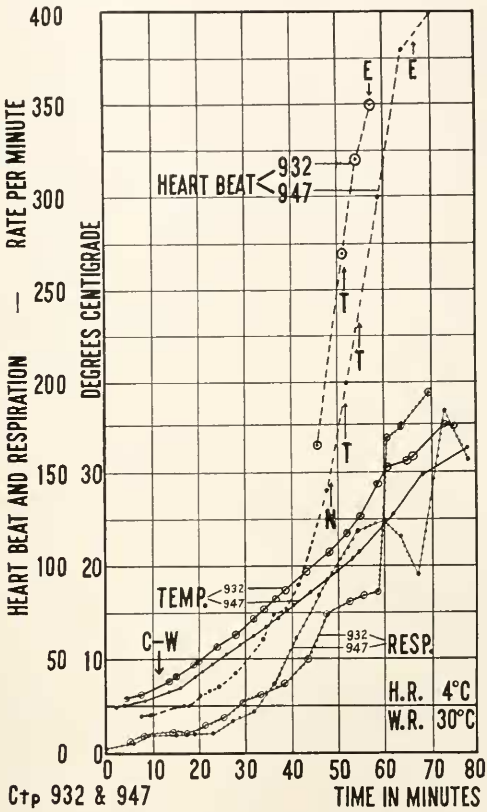

FIG. 4. Curves of rise in respiration, heart beat and temperature of *C. t. pallidus* 932 and 947 taken at the same time. The heart beat of 947 was taken with a needle to *N*, then with a stethoscope. A stethoscope alone was used on 932. *H. R.*, hibernating room; *C. W.*, point of transfer of animals from a room of 10° C. to a warm room (*W. R.*) of 30° C.; *T*, trying to turn over on feet; *E*, eyes opened.

Figure 5 illustrates two cases of waking of *C. t. pallidus* animals in which the heart beat was determined with an electrocardiograph. The electrodes were wound about the fore legs of Ctp 734 three minutes before the beginning of the record as given in the graph. The animal was transferred from a temperature of

7° to one of 17° C. at three minutes in Fig. 5. When the electrodes were placed on the fore legs the animal moved only very slightly but the respiration rose from an average of about two to

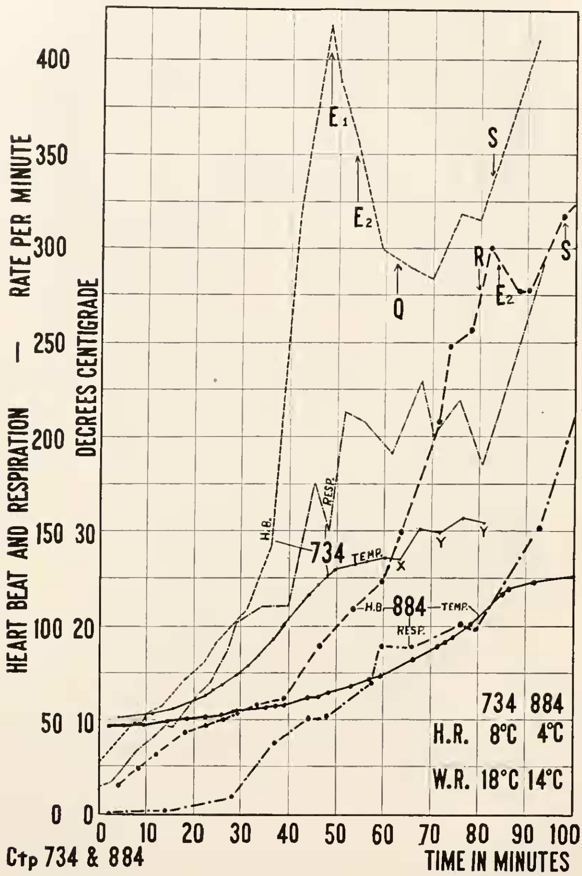

FIG. 5. Curves of rise in respiration, heart beat and temperature of *C. t. pallidus* 734 and 884, in which the heart beat was determined with the aid of an electrocardiograph. Both animals were straightened out, electrodes placed on the fore legs, thermocouple inserted into the food pouch and the animal laid on its back or side in the nest. *H. R.*, hibernation room; *W. R.*, waking room; E_1, first eye open; E_2, both eyes open; *Q*, quiet; *S*, struggling; *R*, righting, turning over on feet; *x*, thermocouple partly out of food pouch; *y*, thermocouple probably partly out.

seventeen a minute. Owing to the fact that all the observations were made by the author unaided and also to the fact that the thermocouple did not remain completely in the pouch after the animal opened its eyes the temperature curve is not smooth as in practically all other graphs. It should be noted that this record is carried further past the opening of the eyes than in the other graphs. This accounts for the fluctuations in heart beat and respiration in the last 50 minutes.

Ctp 884 was removed from an outdoor temperature of 4° to a room temperature of 13° C. at the beginning of the record shown in Fig. 5. This animal was not disturbed much by the electrodes being placed on the fore legs. Probably partly on this account and partly on account of the colder room it woke more slowly than Ctp 734. However, internal conditions may have been influential also, as indicated in some other waking records in which an animal would wake much less readily than usual.

It is to be noted in all cases (Figs. 1, 3, 4) that the heart beat rises very rapidly once it has reached 200 or 250 a minute shortly before the opening of the eyes.

Since some observers (*e.g.*, Hall, '32) have intimated that a rapid increase in respiration as soon as the animal is disturbed is the cause of waking, an attempt was made to determine whether heart beat or respiration took the lead in waking. Fourteen graphs of waking in a cold room (1° to 12° C.) show the heart beat and respiration rising before the temperature in practically all cases. It was difficult to determine accurately whether heart beat or respiration rose first, but in about eight or nine cases the heart beat appeared to rise first, and in two or three cases respiration appeared to rise before the heart beat.

In the warm room of about 29° C. the temperature rose first in practically all of the eight graphs studied, and heart beat rose before respiration in all but one case. In a room of about 20° C. the temperature rose first in four out of eleven cases, temperature and heart beat rose together in three others and in one or two cases the heart beat rose first. Respiration was usually last to rise (seven in eleven cases). In two or three cases all three rose at about the same time.

In an electrocardiograph record of a *C. t. pallidus* the heart beat appeared to rise before the respiration when disturbed outdoors (5° C.) and fell first of the two as the animal went back into deep hibernation. Four hours later when removed to a room of 18° C. heart beat again rose in advance of respiration. In this animal the heart missed a beat more or less frequently, as seen in Fig. 6 which is shown here because the missing of beats was not uncommon and sometimes caused abnormal awakening. (No such records have been included elsewhere in this paper.) After reaching a rate of 63 a minute at 7:25 P.M. the rate fell to 50, 44 and 20 a minute at 7:29, 7:35 and 7:42 P. M., respectively (see Fig. 6, *a*, *b*, *c*).

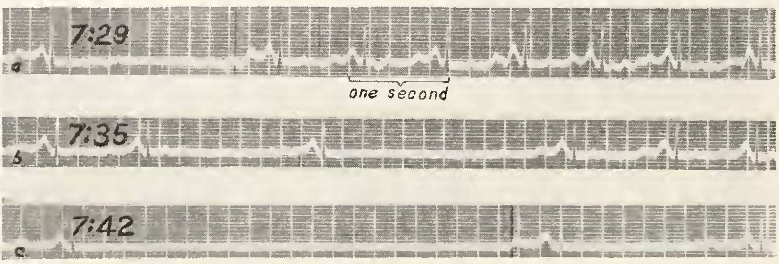

Fig. 6. Electrocardiograms of Ctp 938 showing how heart beat may fall abnormally in rate from a missing of beats after waking from hibernation has begun.

The respiration increased some after the heart beat had begun to fall, but 18 minutes after the highest heart beat the respiration had reached its highest point and took a rapid fall, remaining low in spite of the gradual warming of the animal by the room temperature (18° C.).

On a previous day (on which it showed no irregularity of heart beat) the same animal after partially awakening in a warm room showed an earlier drop in heart beat rate than in respiration when the room was rapidly cooled. During two hours of gradual warming of the room from 12° to 22° C. the heart beat rose gradually from 12 to 36 while the respiration continued at about 5 a minute. Near the end of that time the respiration showed one rise to 20 and another to 15 a minute.

While it is difficult to attribute a leading rôle to either respiration or heart beat in waking, it seems that the heart usually initiated the process to a greater extent than respiration when the animal was disturbed in a cold room. In a warm room waking was chiefly induced by a rise in body temperature followed by an increase first in heart beat and then in respiration.

In several records respiration rose when the animal was disturbed but fell again in a few minutes, whereas the heart once started to beat faster tends more to accelerate and produce waking, as if once started to beat faster it could not decrease in rate again till waking has occurred.

The Effect of Stimulation upon the Rate of Waking.

Since it was evident that waking usually followed disturbing the animal by taking its temperature even in the cold room, it was thought that stimulation of the torpid animal would show whether heart beat or respiration was first to respond and therefore leading in the waking process. The results of a number of experiments were not very clear cut. It became evident that while stimulation of some sort usually starts the waking process, the rate of waking is not increased in proportion to the increase in amount of stimulation.

Electrical stimulation (rapid make and break shocks with a Harvard inductorium using one dry cell of 1.5 volts with the secondary coil of the inductorium set at 6 cm.) was applied to four animals a total of eleven times for a few seconds each time. Heart beat increased in four cases, decreased in three, and remained the same in three. The respiration rate increased in five cases, decreased in four cases and did not change in two cases. In one animal which did not awaken the respiration fell to 0 for a minute following six out of seven stimulations. Heart beat also was retarded in three out of the seven stimulations.

Stimulation by dropping a 5 gram weight on the animal every ten seconds from a height of five inches appeared to slightly accelerate the rate of waking, but this was only slight for the opening of the eyes occurred about the same time as in the controls in three experiments of four to eight animals each.

The continuous ringing of an electric door bell suspended near the animals had no noticeable effect on three animals as compared with their controls. Ringing for six-minute periods inhibited respiration and heart beat for a minute after the bell was started for the first two ringings. In another animal which was waking more rapidly than usual the sound of the bell did not check heart beat and apparently accelerated respiration.

Handling the animal did not always produce waking. In a room where the temperature was falling the insertion of a thin flexible thermocouple into the cheek pouch of a torpid animal did not usually cause it to wake, though a slight temporary rise in respiration and temperature was often observed. A thermometer bulb inserted into the cheek pouch produced waking. Some animals appeared to wake more readily than others, though this could often be ascribed to a difference in body temperature at the start. One castrated male ground squirrel began to awaken in the cold room, but soon respiration, heart beat and temperature all fell and it became completely torpid again. The animal was disturbed only at first.

The Effect of a Near Freezing Temperature on Waking.

Since Horvath ('81), Dubois ('96), and Pflüger and others (according to Merzbacher, '04) found that temperatures near 0° C. caused hibernating mammals to awake and since ground squirrels appeared to me to hibernate very well below 5° C., two experiments were performed to determine whether there was a difference between species in this regard. At one time six *C. t. pallidus* were transferred from a warmer part of the refrigerator to a colder part (4° at first, falling to 2° C. in 4½ hours). All were still torpid in 85 minutes, but Nos. 1 and 2, which had a higher respiration rate (20 a minute) than the others at first, were awake, and Nos. 3 and 4, which had been deeply torpid, were waking, at 4½ hours. Left over night Nos. 1 and 2 were partly torpid again at a refrigerator temperature of 1° C., and Nos. 3 and 4 were now very deeply torpid, as was also No. 5, but No. 6 was partly torpid and woke before the next day. On the third day Nos. 1, 4 and 5 were very deeply torpid at a refrigerator temperature of 0.85° C. and No. 3 was partly torpid. On the fourth day Nos. 1, 3 and 4 were torpid at a refrigerator temperature of 0.3° C.

At another time the cages of three *C. t. pallidus* were placed on the floor of the very well insulated room at an air temperature of 1° C. and three others left in the refrigerator at 2° to 3° C. All were deeply torpid at first except that one of those removed to the floor was breathing deeper than the others. This and one other on the floor and one in the refrigerator woke within eight hours. The third one on the floor was still torpid the next morning at a room temperature of 0° C., but began to awake in the afternoon. Two in the refrigerator did not wake the first two days. Transferred to the floor one woke the following day.

While many of the animals in these experiments woke from hibernation when transferred to a room of within a degree of freezing, this did not occur to the extent claimed for the marmot by Dubois ('96), nor did this temperature hinder a return to the hibernating state in ground squirrels. An examination of his plates 4 and 5 show that the buccal temperature rose from the first. This fact suggests strongly that waking was produced partly by the mechanical stimulation involved in taking the rectal temperature and in transferring the animal to the colder room. The same two sources of stimulation were present in Horvath's ('81) experiments. Further evidence that waking from hibernation does not always occur was found in the death of a number of hibernating ground squirrels in the early part of the work when attendants permitted the room temperature to fall to or below freezing.

Discussion.

A continuance of hibernation appears to be dependent upon the absence of external and internal stimuli, for waking is readily induced by mechanical or electrical stimuli or by warming. Since some animals wake more readily than others internal conditions appear also to influence waking. This is also indicated by the awakening at intervals of a few days of many hibernating animals.

Heart beat appears to increase somewhat more than respiration at the beginning of waking and, therefore, seems to have more influence on waking than does respiration. The interesting condition of inhibition of respiration producing inhibition of heart beat in the duck shown by Dooley and Koppanyi ('27) was kept in mind during this study of waking from hibernation, but heart beat seemed to rise independently of respiration, not only in ordinary waking but also in a case where the thorax was cut open so that the animal could not secure air. This animal had a higher rate of heart beat when it was warmed, rising from 4 to 28 a minute in 37 minutes in one animal transferred from a surrounding temperature of 4° to one of 18° C. Such an animal could probably not become much warmer than the room because of the lack of oxygen in its blood.

At no time in waking were heart beat and respiration at the same rate, but sometimes the two would occur together, a condition claimed to be common in deep torpor by Dubois ('96) in the marmot. He also thought that the heart beat was augmented when it occurred at the same time as an inspiration suggesting a causative relation of respiration to heart beat. No such increased beat of the heart was apparent when it occurred at the same time as a respiration in the torpid ground squirrel.

The rise of temperature in a torpid animal in a cold room is slow at first because respiration and heart beat increase only very gradually and, therefore, there is little increase in heat produced. It is generally considered (Bayliss, '18, p. 455) that muscular contraction is the "chief if not the only, source of heat of practical importance to the animal organism."

Since contact or electrical stimulation usually causes waking of the torpid animal, the question arises why persistence of stimulation during waking does not speed up the process greatly. That it does not do this at all in proportion to the amount of stimulation, suggests the "all or nothing" principle. This principle would not seem to hold in an exact way, but waking is nearly always completed when once started, and the rate may not be increased much by added stimuli. One reason that the rate is not modified greatly by stimulation is probably the inability of muscle to contract rapidly when cold as observed by electrical stimulation of the muscles through the skin. The acceleration of the waking process by warming and the retardation by cooling the animal support this, as does also the regaining of motility in the anterior (warmer) regions of the body at an earlier time than in the posterior (colder) portion of the body in waking. At the very beginning of waking from deep hibernation there is usually no response to even severe mechanical stimuli like cutting through the body wall, indicating that such stimuli do not pass through the central nervous system, but as waking begins and while the animal is still cold (10–15° C.) coördinated responses to electrical and mechanical stimuli appear. These responses are sluggish but fairly vigorous, and lead an observer to expect the stimulated animals to wake up much more rapidly than the controls.

Another factor in the production of a rapid rise of metabolism may be the temperature control mechanism. This appears to be only slightly active in the first part of waking and in quiet awaking does not appear to be so active as in the latter part of stimulated awakening where the shivering and trembling probably produced by the heat regulating system doubtless aid in the production of the very rapid rise in metabolism shown in most of the graphs in this paper. That the heat regulating mechanism is not so active in animals waking undisturbed in a warm or cold room may be indicated by the almost entire absence of shivering and shaking.

The production of a torpid state in cats by means of anæsthesia by Britton ('22) and the gradual recovery that resembles waking from hibernation tends to bear out the idea that the muscles of the heart and thorax are inhibited by cold and have grades of functioning according to their temperature, which also appears to be true of cold blooded animals. Britton could not produce a state of artificial hibernation but found that the cats would either die or very slowly awake from a body temperature of about 19° C. in a room of the same temperature. An experiment in which the temperature of the ground squirrel was lowered by means of ether anæsthesia to 22.8° C. was performed by the author before he knew of Britton's work. Spontaneous awakening took place. Many interesting comparisons might be worked out between the cooling of a cat or other homoiothermal animal and of a hibernating mammal. It should be noted that Horvath ('81) found that the hibernating animal had the ability to survive when the body temperature is lowered in ice water to much below 19° C. without artificial respiration, whereas non-hibernating forms (dog, rabbit) died if subjected to temperatures below 19° C. without artificial respiration (Horvath, '76). If artificial respiration was kept up the rabbit heart stopped beating at 9° C., whereas in the hibernating animal it did not stop at 4° or even 2° C. (Horvath, '81).

Summary.

The increase in respiration, heart beat and temperature as shown in graphs is very gradual at first in waking in a cold room of 0° to 8° C., whereas in a warm room of near 30° C. the process is more rapid from the first. In both cases there is a very rapid rise of all near or at the time of the opening of the eyes when the respiration rate commonly ranged between 100 and 200 a minute, and the heart beat rate usually ranged between 300 and 400 a minute, and the temperature between 20° and 34° C. The anterior part of the animal wakes more rapidly than the posterior regions, and œsophageal and food pouch temperatures indicate the increase in metabolism more accurately than deep rectal or anal temperatures. There is a general correlation between the curves of rise of respiration, heart beat and temperature. In the production of waking heart beat appears to be somewhat more effective than respiration. Waking may be induced by stimulation but its rate is not proportional to the duration or intensity of the stimulation applied, except in the case of a surrounding high temperature. Transference to a room of about 0° C. appears to stimulate waking in some but not in all torpid ground squirrels. This temperature does not prevent hibernation.

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